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34. Longevity, mortality and disease

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Introduction

Demographic studies of natural populations are important in determining the role played in the community by each taxon. Of particular interest are the survival rates on a temporal basis with regard to age structure. In this chapter we shall deal with mortality (the reciprocal of survival), longevity, and factors which may effect mortality (such as disease).

Desert ecosystems present a rigorous environment in which to live, yet afford a wide variety of ecological niches to occupy. Consequently it is not unusual to encounter a diversity of animals seldom found in more predictable environments. Although deserts offer a unique natural laboratory to study demographic parameters under such diverse conditions, there is a dearth of comprehensive studies in the literature. Thus we must draw heavily on the literature from other communities to arrive at generalizations which may or may not apply to desert communities. For the most part we limit our discussion to methodologies and generalizations and then present the data available for North American deserts.

In many studies of animal populations there is an attempt to determine age structure and mortality. In many taxa and stages of the life cycle, however, information is scanty. Life tables have been constructed for many game animals (see for instance, Green & Evans, 1940; Leopold, Sperry, Feeney & Catenhusen, 1943; Murie, 1944; Caughley, 1966; Bradley & Baker, 1967), but in general there are relatively few such studies on small mammals (see review in Caughley, 1966), small birds (see review in Lack, 1954), other vertebrates (see review in Deevey, 1947) or invertebrates (see review in Harcourt, 1969). Mortality rates during the nestling period of altricial birds are well known (Ricklefs, 1969). The availability of longevity and mortality data depends largely on the ability to sample and age individuals of a population. The occurrence and incidence of disease are even less well known unless the information is of importance to man.

Throughout, daily mortality rates are calculated (Ricklefs, 1969) by:

$$m = \frac{-(\log_e P)}{T}$$

where P is the proportion surviving until time T (in days).

Insect mortality

Little is known concerning mortality of desert insects. The construction of life tables based on demographic data on field populations is mainly restricted to agricultural pests (Harcourt, 1969). The construction of insect life tables requires a sampling procedure that includes a wide variety of growing conditions and the measurement of the mortality factors involved. A detailed account of procedures and calculations is given by Harcourt (1969).

Mortality in the moth, *Plutella maculipennis* in Ottawa, Canada, has been summarized by Harcourt (1969). Loss of eggs was small (1.2%), whereas loss between hatching and the 4th instar rose to 47.0%. Mortality then declined until cocoon formation at which time it increased to 51%. The major mortality factors were rainfall, parasitism and predation, but their relative importance depended on the life stage.

Mortality over a 14-year period in *Bupalus piniarius* (Lepidoptera) in the Netherlands has been summarized by Klomp (1966). Loss of eggs was moderate (36.7%) increasing in the first instar to 53.5%. Mean mortality during intermediate instars was from 17% to 22%, but then increased for prepupal stages (36% to 40%). Mean mortality by midwinter was very low (5.4%) but reached a maximum of 53.3% by spring. Again, factors that affected mortality varied in importance depending on season and stage in the life cycle. Also, vast differences occurred from year to year depending on fecundity and density-independent factors.

The examples given above may give some indication as to the variability in mortality rates in insects. Unfortunately, no such studies exist for desert-dwelling insects. Preliminary mortality data on the lepidopteran *Aroga websteri*, reared in the laboratory, have been collected by Hsiao & Green (1974). Mortality followed trends similar to those illustrated above with high losses in early larval stages (58% to 66%), whereas losses decreased to 18% prior to pupation. Pupal mortality amounted to 43.2%. The total loss attributed to parasitism amounts to 20.2%, but the major mortality appeared to arise from other causes, for all life stages examined. The laboratory data gathered so far represent good comparative information but point to the dearth of knowledge concerning desert insects.

It is apparent that many factors, singly or in some combination, affect mortality in insects. Differential mortality is found at different life-stages, and density of the population may account for its severity during earlier stages. The methods for determining and analyzing the various factors influencing mortality in insect populations have been discussed by Solomon (1964).

Amphibians

Much of our knowledge of demography of frogs and toads has been summarized by Turner (1962). Life tables for a genus of salamanders have been established by Organ (1961). Survival in adults has been studied by recapture of marked individuals and of larvae by estimates of number surviving from the estimated number of eggs laid. Anuran mortality is relatively poorly known. Mortality of larvae is high (probably averaging more than 90% of eggs laid) and appears to be governed by rainfall, site of oviposition and permanence of the water source (Bannikov, 1948; Martof, 1956a; Turner, 1960; Herreid & Kinney, 1966; Tevis, 1966). More data are available for adult mortality. Conservative estimates of adult mortality to the first year after initial capture ranged from about 40% to 90% in various species (Bannikov, 1950; Blair, 1953; Jameson, 1955, 1956b; Pearson, 1955, 1957; Martof, 1956b; Turner, 1959, 1960; Kelleher & Tester, 1969). Mortality appears to be age-specific, at least in some species, with juveniles and older adults experiencing greater mortality than first-year adults (Bannikov, 1950; Jameson, 1956b; Kelleher & Tester, 1969). Jameson (1955) found greater mortality during the summer than winter in *Syrhophus marnocki*.

Studies of desert anurans are few (Table 34.1). Turner (1959) estimated an annual adult mortality of 56% (0.22% per day) for *Bufo punctatus* in Death Valley. High mortality rates of larval stages of the same species were noted in another California desert site by Tevis (1966). Toads of the genus *Scaphiopus* are well-adapted to and widespread in North American deserts. Although there have been no studies of desert populations, an investigation of a member of this genus in Florida indicated an annual adult mortality rate of less than 40% (Pearson, 1955). Desert species are probably similar.

The most important factor which affects anuran mortality appears to be the availability and, especially in arid lands, permanence of water (Bragg, 1940; Jameson, 1956a, b; Martof, 1956b; Turner, 1960; Tevis, 1966). Other mortality factors include abnormalities in development, fungal infestations, temperature (Herreid & Kinney, 1966), predation (Bragg, 1940; Jameson, 1956b), crowding, and pollution (Bragg, 1940). Pearson (1955) found the greatest survival of adults of *Scaphiopus h. holbrooki* at intermediate densities, suggesting that density-dependent factors may be involved.

Longevity of captive anurans ranges from 11 years in Pelobatidae and 16 years in Hylidae and Ranidae to more than 30 years in Bufonidae (Goin & Goin, 1962). Natural longevity is considerably less (Table 34.1) with values of about 9 years in Pelobatidae (Pearson, 1955), 3 to 4 years or more in Bufonidae (Hamilton, 1955; Thornton, 1960; Tevis, 1966), 3 to 5 years

Table 34.1. Mortality and longevity of some desert amphibians and reptiles

Species	Annual mortality of adults (%)	Daily mortality rates (%)			Maximum natural longevity	Average age of breeding population (months)	Location	Source
		First week	Juveniles (age)	Adults (age)				
Amphibia								
Pelobatidae								
<i>Scaphiopus couchi</i>	47	—	—	0.17 (1-2 yr)	> 2 yr	—	Texas	Jameson, 1956a
Bufonidae								
<i>Bufo woodhousei</i>	—	—	—	—	> 4 yr	—	Texas	Thornton, 1960
<i>Bufo punctatus</i>	56	—	—	0.22 (1-2 yr)	> 4 yr	—	California	Turner, 1959; Tevis, 1966
Microhylidae								
<i>Gastrophryne olivacea</i>	—	—	—	—	7-8 yr	—	Kansas	Fitch, 1956b
Reptilia								
Testudinidae								
<i>Gopherus agassizi</i>	5	—	—	—	> 30 yr	—	Utah	Woodbury and Hardy, 1948
Iguanidae								
<i>Sauromalus obesus</i>	5-25	—	—	< 0.01	—	—	California	Berry, 1974
<i>Crotaphytus collaris</i>	55	—	0.30 (< 10 m)	0.20 (> 10 m)	—	—	Kansas	Fitch, 1956a
<i>Crotaphytus wislizenii</i>	38	—	0.40 (< 8 m)	0.13 (> 8 m)	7-8 yr	—	Nevada	Turner <i>et al.</i> , 1969
<i>Crotaphytus wislizenii</i>	57	—	0.52 (< 8 m)	0.23 (> 8 m)	7-8 yr	—	Nevada	Turner <i>et al.</i> , 1969
<i>Sceloporus magister</i>	—	—	—	—	> 6 yr	—	Nevada	Tanner and Krogh, 1973
<i>Sceloporus undulatus</i>	71	—	1.11 (0-1 yr)	0.33 (> 1 yr)	> 3 yr	—	New Mexico	Vinegar, 1975
<i>Sceloporus undulatus</i>	72	—	1.34 (0-1 yr)	0.35 (> 1 yr)	—	—	New Mexico	Vinegar, 1975
<i>Uta stansburiana</i>	91	6.15	1.70 (2-8 wk)	0.54 (8-52 wk)	22 m	9	Texas	Tinkle, 1967

<i>Uta stansburiana</i>	91	6.82	2.16 (2-8 wk)	0.54 (8-52 wk)	32 m	9	Texas	Tinkle, 1967
<i>Uta stansburiana</i>	78	—	0.78 (2-10 wk)	0.41 (> 10 wk) ⁽¹⁾	—	12	Colorado	Tinkle, 1967
<i>Uta stansburiana</i>	78	—	0.66 (< 8 m)	0.40 (> 8 m) ⁽²⁾	44 m	12	Nevada	Turner <i>et al.</i> , 1970
<i>Uta stansburiana</i>	67	—	0.35 (< 8 m) ⁽³⁾	0.30 (> 8 m) ⁽⁴⁾	—	11+	Nevada	Turner <i>et al.</i> , 1974
<i>Uta stansburiana</i>	—	—	0.79 (< 8 m)	—	—	—	Nevada	Turner <i>et al.</i> , 1974
Xantusiidae								
<i>Xantusia vigilis</i>	29	—	—	0.09 (36-72 m)	—	—	California	Zweifel and Lowe, 1966
<i>Xantusia vigilis</i>	50-95	—	—	0.18-0.82 (72-108 m)	—	—	California	Zweifel and Lowe, 1966
Teiidae								
<i>Cnemidophorus tigris</i>	43	—	0.27 (< 8 m)	0.15 (> 8 m)	7 yr	22	Nevada	Turner <i>et al.</i> , 1969a
<i>Cnemidophorus tigris</i>	41	—	—	—	—	—	Nevada	Tanner and Jorgensen, 1963
Colubridae								
<i>Masticophis taeniatus</i>	—	—	—	0.23 ⁽⁵⁾	—	—	Utah	Hirth, 1966
Viperidae								
<i>Crotalus viridis</i>	78	—	0.29 (< 2 yr)	0.05 (> 3 yr)	> 10 yr	—	Utah	Woodbury <i>et al.</i> , 1951

⁽¹⁾ Based on annual survival rate from overwinter survival of juveniles (6 m) and recaptures of adults in their second season (12 m).

⁽²⁾ Females from Table 8, Turner *et al.*, 1970

⁽³⁾ Enclosures with predatory *Crotaphytus wislizenii* excluded.

⁽⁴⁾ Average from Table 10, Turner *et al.*, 1974.

⁽⁵⁾ From overwinter survival.

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in Hylidae (Jameson, 1956a; Green, 1957) and 5 to 12 years in Microhylidae and Ranidae (Fitch, 1956b; Martof, 1956a; Turner, 1960).

Reptiles

Data on mortality in lizard populations are obtained mainly through marking and subsequent recovery. Mortality rates are known from many intensive studies (Stebbins & Robinson, 1946; Fitch, 1954, 1956a, 1958; Crenshaw, 1955; Blair, 1960; Hirth, 1963; Zweifel & Lowe, 1966; Tinkle, 1967; Brooks, 1967; Turner, Lannom, Medica, & Hoddenbach, 1969; Turner, Medica, Lannom & Hoddenbach, 1969a, b; Turner, Hoddenbach, Medica & Lannom, 1970; Turner, Medica & Smith, 1973, 1974). Most of these concern species whose ranges include the desert, although some studies were of non-desert populations (Table 34.1). Annual mortality rates vary considerably from a nearly annual turnover in some populations of *Uta stansburiana* (Tinkle, 1967) to an annual mortality of less than 30% during the first few years of life in *Xantusia vigilis* (Zweifel & Lowe, 1966), and between 5% and 25% in *Sauromalus obesus* (Berry, 1974). Variation also exists between populations of a single species and in successive years as illustrated by *Uta stansburiana* (Tinkle, 1967; Turner *et al.*, 1970, 1974). Studies of non-desert species indicate similar ranges of annual mortality (Kramer, 1946, cited by Lack, 1954; Crenshaw, 1955; Kennedy, 1958; Fitch, 1958, 1967; Hirth, 1963; Sexton, Heatwole & Meseth, 1963; Storr, 1965; Brooks, 1967).

Mortality of eggs and newly hatched young is poorly known. Blair (1960) reported a (maximum) 76.6% nest mortality (2.42% mortality per day assuming a 60-day incubation period). Of eggs which survived the incubation period, 6.4% failed to hatch (0.10% per day). Thus mortality during incubation averaged 78% (2.52% per day). In contrast, about 50% of eggs laid by *Crotaphytus collaris* hatched (Fitch, 1956a). During the first few days after hatching mortality rates of *Uta stansburiana* were high (> 6% per day (Tinkle, 1967)); this decreased in juveniles to a level somewhat higher than in adults (Table 34.1).

Predation by other lizards, snakes and occasional mammals and birds appear to be the major mortality factor in lizards (Blair, 1960; Tinkle, 1967; Brooks, 1967; Turner *et al.*, 1974). At least in some species, mortality is density-dependent (Turner, Lannom, Medica & Hoddenbach, 1969; Turner *et al.*, 1973). Severe winter weather accounted for deaths of about 25% of a *Uta stansburiana* population (Tinkle, 1967).

Longevity is known for several species, mostly from captive individuals. Available data indicate that potential longevity averages about 6 to 7 years in Agamidae and Gekkonidae, 15 years in Iguanidae and Teiidae and 20 years in Scincidae and Helodermatidae (Altman & Dittmer, 1962). Actual

longevity in the wild averages 3 to 8 years in Iguanidae and 7 years in Teiidae (Table 34.1). Average age of a population of *Uta stansburiana* was estimated as 18.5 weeks (Tinkle, 1967). Average age of the breeding population increases with decreasing annual mortality (Table 34.1). An adult population of *Sceloporus magister* in Nevada consisted mainly of individuals 3 to 5 years old (Tanner & Krogh, 1973), indicating a low annual mortality rate.

Data for reptiles other than lizards are few. Woodbury & Hardy (1948) estimated mortality at less than 5% per year for *Gopherus agassizi*. Snake mortality was heaviest during the first 1 or 2 years of life, declining to very low rates among sub-adults and adults (Fitch, 1949; Woodbury *et al.*, 1951). Overall mortality rates for three species of snakes during approximately 7 months of hibernation averaged 0.23% per day (Hirth, 1966). Of two species which range into the Great Basin Desert, *Masticophis taeniatus* averaged 0.23% mortality per day and *Crotalus viridis* 0.19% per day.

Tortoises are long-lived, but longevity of *Gopherus agassizi* appears unknown although it is in excess of 30 years (Patterson & Brattstrom, 1972). Longevity of captive snakes is in excess of 20 years (from summarization by Goin & Goin (1962)).

Birds

Adult mortality and longevity

Adult mortality rates for birds have been obtained mainly through banding individuals of known age and their subsequent recovery as recaptures, census of marked individuals returning to a specified area to breed, or recoveries of dead birds. Adult mortality in stationary populations can be derived from the number of new breeding birds each year by assuming that replacements equal adult mortality. Adult mortality rates are known for a number of species of birds (see reviews by Hickey (1952, 1955), Lack (1954), Farner (1955), Boyd (1962), Ashmole (1971) and Botkin & Miller (1974)). Among passerines of the temperate zone, annual adult mortality averages 40% to 60% (Lack, 1954), while that for gallinaceous species averages 50% to 80% (Hickey, 1955). Annual adult mortality rates among desert passerines appear slightly lower, judging from the few data available for North American species: about 40% in *Auriparus flaviceps* (based on the proportion of first-year birds at the beginning of the breeding season (Austin, 1977)), about 39% in *Campylorhynchus brunneicapillus* (based on the mean approximate proportion of year-old individuals in the male population (Anderson & Anderson, 1973)) and about 48% in *Toxostoma curvirostre* (based on loss of winter-banded birds (Anderson & Anderson, 1973)).

Numerous data are available on longevity of birds, both in captivity and

Table 34.2. Nesting success of birds in North American deserts. (Fledging success = percent eggs laid to fledge; nest success = percent nests built to fledge at least one young)

Species	Fledging success	Nest success	Number of nests	Habitat	Year	Location	Source
Columbidae							
<i>Zenaidura macroura</i>	32.4	26.1	46	Desert grassland	1970-71	Arizona	Austin, unpublished data
	14.3	15.0	20	Desert scrub	1971-72	Arizona	Russell <i>et al.</i> , 1972, 1973
<i>Zenaidura asiatica</i>	40.9	41.7	24	Desert scrub	1948-49	Arizona	Hensley, 1954
Paridae							
<i>Auriparus flaviceps</i>	44.1	54.2	48	Desert grassland	1970-71	Arizona	Austin, 1977
	29.7	36.0	25	Desert scrub	1965-66	Arizona	Taylor, 1971
	82.1	80.0	15	Desert scrub	1948-49	Arizona	Hensley, 1954
	83.2	100.0	25	Desert riparian	1969-70	Nevada	Austin, 1977
	56.9	—	18	Desert scrub	1965	New Mexico	Moore, 1965
Troglodytidae							
<i>Campylorhynchus brunneicapillus</i>	47.8	55.7	61	Desert grassland	1970-71	Arizona	Austin, unpublished data
	54.3	66.0	53	Desert scrub	1939-59	Arizona	Anderson & Anderson, 1973
	64.6	68.8	154	Desert scrub	1963-68	Arizona	Anderson & Anderson, 1973
	82.6	80.0	20	Desert scrub	1948-49	Arizona	Hensley, 1954
	31.7	46.2	13	Desert scrub	1971-72	Arizona	Russell <i>et al.</i> , 1972, 1973
Mimidae							
<i>Mimus polyglottos</i>	21.6	21.4	14	Desert grassland	1970-71	Arizona	Austin, unpublished data
<i>Toxostoma curvirostre</i>	24.2	24.4	45	Desert grassland	1970-71	Arizona	Austin, unpublished data
	24.4	20.9	86	Desert scrub	1963-68	Arizona	Anderson & Anderson, 1973
	72.5	80.0	15	Desert scrub	1948-49	Arizona	Hensley, 1954
	30.8	31.8	22	Desert scrub	1971-72	Arizona	Russell, <i>et al.</i> , 1972, 1973
Sylviidae							
<i>Poliioptila melanura</i>	0.0	28.6 ⁽¹⁾	14	Desert grassland	1970-71	Arizona	Austin, unpublished data
	20.0	5.0	20	Desert scrub	1971-72	Arizona	Russell <i>et al.</i> , 1972, 1973
Icteridae							
<i>Molothrus ater</i>	22.7 ⁽²⁾	—	—	Desert grassland	1970-71	Arizona	Austin, unpublished
Fringillidae							
<i>Carpodacus mexicanus</i>	80.5	80.0	10	Desert scrub	1948-49	Arizona	Hensley, 1954
<i>Pipilo fuscus</i>	44.0	42.5	40	Desert grassland	1970-71	Arizona	Austin, unpublished data
<i>Aimophila carpalis</i>	42.0	39.0	41	Desert grassland	1970-71	Arizona	Austin, unpublished data
<i>Aimophila cassinii</i>	62.5	63.6	11	Desert grassland	1970-71	Arizona	Austin, unpublished data
<i>Amphispiza bilineata</i>	58.3	60.0	10	Desert grassland	1970-71	Arizona	Austin, unpublished data
<i>Spizella breweri</i>	—	19.4	31	Desert scrub	1972	Utah, Idaho	Balch, 1973

⁽¹⁾ Successfully raised *Molothrus ater*.

⁽²⁾ From nests of *Poliioptila melanura*, *Vermivora luciae*, *Aimophila carpalis*, *Aimophila cassinii*, and *Amphispiza bilineata*.

Table 34.3. Mortality rates of North American desert birds (percent per day)

Species	Stage of Life Cycle				Location	Year	Source
	Egg	Nestling	Post-fledging ⁽¹⁾	Adult			
Columbidae							
<i>Zenaidura macroura</i>	5.95	1.07	—	—	Arizona	1970-71	Austin, unpublished data
	6.18	7.96	—	—	Arizona	1971-72	Russell <i>et al.</i> , 1972, 1973
<i>Zenaidura asiatica</i>	2.81	0.87	—	—	Arizona	1948-49	Hensley, 1954
Paridae							
<i>Auriparus flaviceps</i>	2.56	1.86	0.87	—	Arizona	1970-71	Austin, 1977
	3.77	2.88	—	—	Arizona	1965-66	Taylor, 1971
	0.19	0.88	—	—	Arizona	1948-49	Hensley, 1954
	0.34	0.66	—	—	Nevada	1969-70	Austin, 1977
	—	—	—	0.13 ⁽²⁾	North American deserts	—	Austin, 1977
Troglodytidae							
<i>Campylorhynchus brunneicapillus</i>	1.66	2.11	0.84	—	Arizona	1970-71	Austin, unpublished data
	2.30	1.02	—	—	Arizona	1939-59	Anderson & Anderson, 1973
	1.01	1.22	2.21 ⁽³⁾	0.14 ⁽⁴⁾	Arizona	1963-68	Anderson & Anderson, 1973
	2.19	3.65	—	—	Arizona	1971-72	Russell <i>et al.</i> , 1972, 1973
	0.82	0.17	—	—	Arizona	1948-49	Hensley, 1954
Mimidae							
<i>Mimus polyglottos</i>	4.44	7.21	—	—	Arizona	1970-71	Austin, unpublished data
<i>Toxostoma curvirostre</i>	4.13	4.71	1.92	—	Arizona	1970-71	Austin, unpublished data
	4.03	5.63	6.35 ⁽⁵⁾	0.19 ⁽⁴⁾	Arizona	1963-68	Anderson & Anderson, 1973
	2.09	5.08	—	—	Arizona	1971-72	Russell <i>et al.</i> , 1972, 1973
	0.51	1.43	—	—	Arizona	1948-49	Hensley, 1954
Icteridae							
<i>Molothrus ater</i>	8.18	3.06	—	—	Arizona	1970-71	Austin, unpublished data
Fringillidae							
<i>Carpodacus mexicanus</i>	1.55	0.00	—	—	Arizona	1948-49	Hensley, 1954
<i>Pipilo fuscus</i>	2.50	3.82	—	—	Arizona	1970-71	Austin, unpublished data
<i>Aimophila carpalis</i>	4.71	1.95	1.80	—	Arizona	1970-71	Austin, unpublished data
<i>Aimophila cassinii</i>	1.28	3.08	—	—	Arizona	1970-71	Austin, unpublished data
<i>Amphispiza bilineata</i>	2.70	1.34	—	—	Arizona	1970-71	Austin, unpublished data

⁽¹⁾ To 30 days post-fledging.⁽²⁾ Based on immature-adult ratios.⁽³⁾ Based on Figure 16-2, Anderson & Anderson (1973).⁽⁴⁾ Based on proportion of first year males in male population, Anderson & Anderson (1973).⁽⁵⁾ Based on Anderson & Anderson (1973), data on p. 185.

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in the wild. Potential longevity of small land birds averages 15 to 20 years in captivity and about 10 years in the wild (from summarization by Altman & Dittmer (1962)). Average age of most small land birds in the wild, however, is approximately 1 to 2 years (Lack, 1954). Among desert species, *Campylorhynchus brunneicapillus* lives at least 5 years in the wild and attain an average age of 1.5 to 2 years, and two individuals of *Toxostoma curvirostre* lived through at least six breeding seasons (Anderson & Anderson, 1973).

Nesting mortality

Mortality during the nesting stage of birds is determined by direct observation of the fate of eggs and nestlings. Nesting success and mortality rates of eggs and young are better known than adult mortality rates, both for birds in general (reviews by Kalmbach (1939), Kendeigh (1942), Lack (1954), Hickey (1955), Nice (1957), Skutch (1966) and Ricklefs (1969)) and for desert species (Tables 34.2, 34.3). In deserts, nesting success is, on the average, lower than the average 55 to 60% for most temperate and arctic species (nest success as cited by Ricklefs (1969, 1973)) but comparable with 21% nest success in a temperate non-desert scrub habitat (Nolan, 1963), 35% fledgling success in a temperate grassland site (Wiens, 1973) and 31% nest success in a humid tropical site (Ricklefs, 1969). Because nestling periods are generally shorter in arid regions (Table 10 in Ricklefs (1969)), mortality rates are, on average, greater.

Considerable variation exists between sites, even in the same desert (Table 34.4), and between years (Marchant, 1960; Lloyd, 1960; Russell, Smith, Gould & Austin, 1972; Russell, Gould & Smith, 1973; Austin, unpublished data). Seasonal variation also exists; in Sonoran Desert grassland, overall nesting success was, on the average, greater after the summer rains than before (Austin, unpublished data). Other factors affecting nesting success in deserts include nest-type (enclosed nests more successful than open nests (Russell *et al.*, 1972; Austin, unpublished data) as in other communities (Ricklefs, 1969)), and nest-orientation (Austin, 1974, 1976).

Mortality factors for eggs and nestlings have been analyzed for a number of passerine species (Ricklefs, 1969), with predation accounting for nearly 55% of egg losses and 56% of nestling losses. In Sonoran Desert grassland, predation accounted for about 30% of egg losses and about 65% of nestling losses (Austin, unpublished data), while other important sources of egg losses were hatching failure, brood parasitism and desertion. In Sonoran Desert scrub, predation (37%) and brood parasitism (22%) were the important causes of nest failure (Russell *et al.*, 1973).

Post-fledging mortality is poorly known for birds as a whole. Mortality

Table 34.4. Average⁽¹⁾ success and mortality of open-nesting birds of arid lands

Hatching success = percent eggs laid to hatch; nestling success = percent eggs hatched to fledge; fledging success = percent eggs laid to fledge; nest success = percent nests built to fledge at least one young.

Location	Average hatching success	Average nestling success	Average fledging success	Average nest success	Average daily mortality rates of eggs & nestlings (%)	Source
Arizona (desert grassland)	48.9 (9) ⁽²⁾	69.8 (8)	34.2 (9)	38.2 (8)	3.86 (8)	Austin, unpublished data
Arizona (desert scrub)	72.8 (3)	89.5 (3)	64.6 (3)	67.2 (3)	1.70 (3)	Hensley, 1954
Arizona (desert scrub)	43.4 (3)	60.2 (3)	21.7 (3)	17.3 (3)	5.68 (3)	Russell <i>et al.</i> , 1972, 1973
S.W. Ecuador (semiarid)	73.2 (11)	70.1 (11)	46.0 (11)	51.6 (11)	3.07 (11)	Marchant, 1960
Iraq	43.9 (8)	59.5 (8)	26.3 (8)	26.9 (7)	4.92 (8)	Marchant, 1963

⁽¹⁾ Mean of values for each species. ⁽²⁾ Number of species involved in calculation.

Table 34.5. Mortality rate of some desert mammals

Species	Annual mortality of adults (%)	Mortality rate per day (%)	Age class	Location	Source
Vespertilionidae					
<i>Eptesicus fuscus</i>	—	0.26	< 1 yr	Minnesota.	Beer, 1955
	—	0.11	1-2 yr	Wisconsin	
	23	0.07	2-10 yr		
Canidae					
<i>Urocyon cinereoargenteus</i>	—	0.27	< 9 m	Georgia.	Wood, 1958
	—	0.33	9-21 m	Florida	
	50	0.19	> 21 m		
Leporidae					
<i>Lepus californicus</i>	—	0.58 ⁽¹⁾	< 10 m	California	Lechleitner, 1959
	60	0.25 ⁽²⁾	> 10 m		
<i>Lepus californicus</i>	—	0.50	first yr	Utah	Gross <i>et al.</i> , 1974
	80	0.44	adult		
Heteromyidae					
<i>Dipodomys merriami</i>	75	0.38	—	Nevada	French <i>et al.</i> , 1967 ⁽³⁾
<i>Dipodomys microps</i>	84	0.50	—		
<i>Perognathus longimembris</i>	62	0.27	—		
<i>Perognathus formosus</i>	70	0.33	—		
<i>Perognathus formosus</i>	58	0.24	> 1 m	Nevada	French <i>et al.</i> , 1974 ⁽⁴⁾
<i>Perognathus formosus</i>	71	0.34	winter	Nevada	Chew <i>et al.</i> , 1973
	75	0.39	summer		
<i>Perognathus parvus</i>	75	0.38	adult		
			1-2 yr	Washington	O'Farrell, Olson, Gilbert & Hedlund, 1975
Bovidae					
<i>Ovis canadensis</i> ♂	—	0.42	< 1 yr	Nevada	Bradley & Baker, 1967
	—	0.01	1-8 yr		
	—	0.06	8-12 yr		
	—	0.25	> 12 yr		

⁽¹⁾ Estimated from calculated annual mortality for adults and age structure in August.

⁽²⁾ Estimated from age structure in February (i.e. 60% of adults replaced in one year).

⁽³⁾ From survival curves 10-30 months, plot A.

⁽⁴⁾ From survival curves through 2 years, plot A and C.

between fledging and independence appears to be lower than mortality in the nest but greater than adult mortality (Table 34.3; see also Lack (1954), Ricklefs (1969, 1973)).

Mammals

Methods for obtaining mortality data for mammals are given by Caughley (1966). Mortality is known for various groups of mammals, but there are insufficient data at present to classify these into discrete patterns.

Table 34.6. Disappearance rates (maximal mortality) of some adult desert rodents

Species	Maximum annual mortality rate (%)	Maximum daily mortality rate (%)	Location	Source
<i>Ammospermophilus nelsoni</i>	60	0.25	California	Hawbacker, 1958
<i>Dipodomys merriami</i>	60	0.25	Arizona	Chew & Chew, 1970
<i>Dipodomys merriami</i>	84	0.51	California	Chew & Butterworth, 1964
<i>Perognathus longimembris</i>	69	0.32	California	Chew & Butterworth, 1964
<i>Peromyscus eremicus</i>	99	1.16	Arizona	Chew & Chew, 1970
<i>Onychomys torridus</i>	77	0.40	Arizona	Chew & Chew, 1970

Demographic parameters are well known for several big-game species (Deevey, 1947; Caughley, 1966; Bradley & Baker, 1967), but the most detailed studies of small mammals have been on laboratory populations (Leslie & Ranson, 1940; Leslie, Tener, Vizoso & Chitty, 1955). Annual mortality rates vary considerably. Rodents generally have high rates of mortality, often with nearly annual population turnover (Linduska, 1947, 1950; Howard, 1949). Annual mortality of lagomorphs is only slightly lower (Green & Evans, 1940; Linduska, 1947; Lechleitner, 1959; Meslow & Keith, 1968; Gross, Stoddart & Wagner, 1974). Bats, carnivores and ungulates experience considerably lower annual mortality (Bourlière, 1947; Deevey, 1947; Beer, 1955; Wood, 1958; Caughley, 1966).

Annual mortality of desert mammals appears similar to figures previously obtained for related species in other temperate communities (Tables 34.5, 34.6). An exception to this is certain Heteromyid rodents (*Perognathus* spp.) that are long-lived and show a relatively low annual mortality for such small mammals (Chew & Butterworth, 1964; French, Maza & Aschwanden, 1967). This has been attributed to their seasonal activity and periods of torpor (Tucker, 1962, 1966; Chew & Butterworth, 1964; French *et al.*, 1967). Periodic torpor during periods of severe weather conditions in the high desert may account for longer life-spans and somewhat decreased mortality in other rodents (e.g., *Dipodomys* spp.).

Prenatal mortality is sometimes estimated by a comparison of numbers of corpora lutea and surviving embryos, and analyzed separately for the pre- and post-implantation periods (Lechleitner, 1959). Few data are available for this category of mortality for mammals in general. In the jackrabbit (*Lepus californicus*) Lechleitner (1959) reported 6% pre-implantational loss and 41.4% post-implantational loss. In the same species, Gross *et al.* (1974) reported a loss of 8% of ova before implantation, and 3% of embryos between implantation and birth. Prewearing

Table 34.7. Longevity and mean age of populations of some mammals which occur in North American deserts

Species	Sex	Maximum Longevity		Mean age of free-living populations	Source
		Captive	Free-living		
Phyllostomatidae					
<i>Macrotus californicus</i>	—	—	40 m	—	Paradiso & Greenhall, 1967
Vespertilionidae					
<i>Myotis lucifugus</i>	—	—	24 yr	—	Griffin & Hitchcock, 1965
<i>Myotis thysanodes</i>	♀	—	11 yr	—	Paradiso & Greenhall, 1967
<i>Myotis velifer</i>	—	—	6 yr	—	Paradiso & Greenhall, 1967
<i>Myotis yumanensis</i>	—	35 m	—	—	Orr, 1958
<i>Pipistrellus hesperus</i>	♂	—	4 yr	—	Paradiso & Greenhall, 1967
<i>Eptesicus fuscus</i>	♂	—	19 yr	—	Paradiso & Greenhall, 1967
<i>Plecotus townsendii</i>	♀	—	16 yr 5 m	—	Paradiso & Greenhall, 1967
<i>Antrozous pallidus</i>	—	8 yr 3 m	—	—	Orr, 1958
<i>Lasiurus cinereus</i>	—	15 m	—	—	Orr, 1958
Molossidae					
<i>Tadarida brasiliensis</i>	—	4 yr 5 m	—	—	Orr, 1958
<i>Tadarida brasiliensis</i>	♂	—	4 yr 6 m	—	Paradiso & Greenhall, 1967
Procyonidae					
<i>Bassariscus astutus</i>	—	8 yr	—	—	Flower, 1931
Mustelidae					
<i>Mephitis mephitis</i>	—	6 yr 1 m	—	—	Flower, 1931
<i>Spilogale putorius</i>	—	9 yr 10 m	—	—	Egocue, Bittmen & Petrovich, 1970
<i>Taxidea taxus</i>	—	13 yr 10 m	—	11 yr	Flower, 1931
<i>Mustela vison</i>	—	10 yr	—	—	Palmer, 1954
Canidae					
<i>Canis latrans</i>	—	15 yr	—	—	Manville, 1953
<i>Urocyon cinereoargenteus</i>	—	> 8 yr 5 m	—	—	Flower, 1931
Felidae					
<i>Felis concolor</i>	—	16 yr	—	9 yr	Flower, 1931
<i>Lynx rufa</i>	—	15 yr	—	—	Flower, 1931
Leporidae					
<i>Lepus californicus</i>	—	> 7 yr	—	—	Haskell & Reynolds, 1947
Heteromyidae					
<i>Perognathus longimembris</i>	♀	7 yr 6 m	—	—	Orr, 1939
<i>Perognathus longimembris</i>	—	8 yr 1 m	—	—	Edmonds and Fertig, 1972
<i>Perognathus longimembris</i>	Both	—	5 yr 1 m	3.8–4.4 m ⁽¹⁾	French <i>et al.</i> , 1967

<i>Perognathus formosus</i>	Both	—	35+ m	3.7–5.0 m ⁽¹⁾	French <i>et al.</i> , 1967
<i>Perognathus formosus</i>	—	—	45+ m	—	Chew <i>et al.</i> , 1973
<i>Perognathus flavus</i>	♀	5 yr	—	—	Aldous, 1930
<i>Perognathus parvus</i>	♀	4 yr 6 m	—	—	Huey, 1959
<i>Perognathus parvus</i>	Both	—	> 3 yr	—	O'Farrell <i>et al.</i> , 1975
<i>Perognathus fallax</i>	♂	8 yr 4 m	—	—	Huey, 1959
<i>Microdipodops megacephalus</i>	—	5 yr 5 m	—	—	Egoscue <i>et al.</i> , 1970
<i>Dipodomys agilis</i>	—	6 yr 3 m	—	—	Rabb, 1960
<i>Dipodomys deserti</i>	—	5 yr 5 m	—	—	Brattstrom, 1960
<i>Dipodomys heermanni</i>	Both	—	—	12 m	Fitch, 1948
<i>Dipodomys heermanni</i>	♂	—	—	35 m	Fitch, 1948
<i>Dipodomys merriami</i>	Both	—	35+ m	3.9–4.7 m ⁽¹⁾	French <i>et al.</i> , 1967
<i>Dipodomys merriami</i>	—	7 yr 9 m	—	—	Egoscue <i>et al.</i> , 1970
<i>Dipodomys microps</i>	Both	—	35+ m	4.9 m ⁽¹⁾	French <i>et al.</i> , 1967
<i>Dipodomys ordii</i>	—	7 yr 5 m	—	—	Egoscue <i>et al.</i> , 1970
Cricetidae					
<i>Reithrodontomys megalotis</i>	—	> 29 m	—	—	Egoscue <i>et al.</i> , 1970
<i>Reithrodontomys megalotis</i>	—	—	—	11 m ⁽²⁾	Svihla, 1931
<i>Peromyscus boylii</i>	—	—	18 m	6.8 m	Brown, 1964
<i>Peromyscus crinitus</i>	—	7 yr 8 m	—	—	Egoscue <i>et al.</i> , 1970
<i>Peromyscus californicus</i>	—	3 yr 6 m	—	—	Egoscue <i>et al.</i> , 1970
<i>Peromyscus maniculatus</i>	♂	8 yr 4 m	—	—	Dice, 1933
<i>Peromyscus truei</i>	—	5 yr 2 m	—	—	Egoscue <i>et al.</i> , 1970
<i>Onychomys leucogaster</i>	—	4 yr 2 m	—	—	Egoscue <i>et al.</i> , 1970
<i>Neotoma lepida</i>	—	5 yr 1 m	—	—	Egoscue <i>et al.</i> , 1970
<i>Neotoma lepida</i>	—	5 yr 7 m	—	—	Rabb, 1960
<i>Lagurus curtatus</i>	—	23 m	—	—	Egoscue <i>et al.</i> , 1970
Tayassuidae					
<i>Tayassu tajaçu</i>	♂	> 9 yr 4 m	—	—	Flower, 1931
Cervidae					
<i>Odocoileus hemionus</i>	—	15 yr	—	8 yr	Flower, 1931
Antilocapridae					
<i>Antilocapra americana</i>	—	15 yr	—	8 yr	Flower, 1931
Bovidae					
<i>Ovis canadensis</i>	♂	17 yr 4 m	16 yr	9 yr 7 m	Bradley & Baker, 1967
<i>Ovis canadensis</i>	♀	—	16 yr	7 yr 3 m	Bradley & Baker, 1967

⁽¹⁾ After logarithmic transformation, data from fenced plots A and C.

⁽²⁾ Captive population.

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mortality is unknown for natural populations but has been estimated as 17% based on laboratory data for *Peromyscus* spp. (French & Kaaz, 1968). Juvenile mortality is also poorly known. In *Lepus californicus*, 80% mortality was reported between birth and March of the following year (Gross *et al.*, 1974). Juvenile mortality in *Lepus* spp. also appears to exceed that of adults (Lechleitner, 1959; Meslow & Keith, 1968). In *Ovis canadensis* juvenile mortality exceeds 70% (Bradley & Baker, 1967).

Longevity, especially in captive mammals, is well known (Table 34.7). Bats are long-lived in the wild, maximum free-living longevities averaging 15 to 20 years. Maximum rodent longevity (in captivity) averages 4 to 7 years; but free-living longevity appears on the average to be less than 2 years, although significant percentages of free-living populations of *Perognathus* spp. may approach potential longevity (Chew & Butterworth, 1964; French *et al.*, 1967).

Disease

The subject of disease naturally follows a discussion of mortality. There are, however, few diseases limited to desert-dwelling animals; therefore, we shall discuss diseases that are common to desert animals yet may be widely spread in other environments. In addition, we are excluding parasitic diseases, inasmuch as a separate chapter would be needed adequately to cover the vast literature on the organisms responsible.

Only three diseases could be considered as specifically 'desert diseases': (a) coccidioidomycosis, (b) desert sore, and (c) West Nile infection (histoplasmosis) (Lowe, 1958). The most serious of the three is coccidioidomycosis, also known as San Joaquin Valley Fever. The disease occurs in all the low-scrub deserts in North and South America and is limited usually, but not exclusively, to the Lower Sonoran Life Zone or its equivalent (Lowe, 1968). This is a highly infectious disease characterized by single or multiple pulmonary and thoracic lymph node granulomas and a tendency to disseminate to other tissues (Merck Veterinary Manual, 1973). *Coccidioides immitis* is the causal, air-borne fungus. As a primary infection it is usually not fatal. However, as a secondary, disseminated lesion it may occur in any organ of the body in any combination of suppuration, necrosis and granuloma. It is the secondary form which may be most important as a factor in mortality. The most recent hypothesis for growth and infection by *C. immitis* involves the intense heating and sterilization of surface soils and seasonal rains promoting rapid germination, growth and reentry of the fungus to the upper soil surface (Lowe, 1968). Dust storms promote the distribution of the infectious spores and their subsequent inhalation by desert animals.

Desert sore is a bacterial skin ulceration usually associated with skin abrasions and poor hygiene (Lowe, 1968). It is of questionable importance in desert animals. West Nile infection is a mosquito-borne arbovirus throughout the desert regions of the Middle East (Lowe, 1968). It is primarily associated with children, and likewise of questionable importance to desert animals in general.

Histoplasmosis is a widespread pulmonary fungal disease similar to coccidioidomycosis caused by *Histoplasma capsulatum* (Merck Veterinary Manual, 1973). This disease is characterized by pulmonary nodules, ulceration of the mucous membranes, and lymphadenopathy. Infection is acquired by inhalation. Chronic infections are not usually fatal; however, acute disseminated histoplasmosis is usually fatal.

There are numerous eye diseases, bacterial and viral, that result in inflammation of the conjunctiva and are collectively termed conjunctivitis. Although this disease is prevalent in human populations it has been found in a variety of other animals (Lowe, 1968; Merck Veterinary Manual, 1973).

Tularemia is a widespread bacterial disease common in rodents and lagomorphs (Lowe, 1968). The causative agent is *Francisella tularensis*, and is spread mainly by ticks. This disease is characterized by fever, lethargy, and lesions of the lymph nodes, liver and spleen (Merck Veterinary Manual, 1973). It may reach epizootic proportions, and may be a periodically important factor in mortality of some small mammals.

Finally, numerous forms of encephalomyelitis can occur in desert animals. Of these, the primary diseases are rabies, Venezuelan equine encephalitis and Western equine encephalitis. These diseases may occur in a variety of desert animals but at present there are no data to assess their impact as a mortality factor.

In summary, there are numerous diseases that occur in desert organisms, but information on them is, in the main, restricted to their relationship to human medicine and general public health. Little is known on the role of these diseases as a factor in mortality of free-living populations.

Conclusions

In general, mortality patterns in free-living animals are poorly known, except for species considered economically important and for nesting mortality in birds. Much of this lack of knowledge is due to the difficulty of studying dispersing populations and thus the low probability of recovering a marked individual, and the length of time necessary to establish mean values of survival in variable ecosystems such as the desert. Certain

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aspects of mortality of free-living populations (preweaning mortality in rodents, for instance) will nearly always have to be extrapolated from laboratory populations or, at best, populations in enclosures.

Within the limits of our knowledge, desert animals follow mortality patterns established for other communities, although there may be more annual variation than elsewhere. Nesting mortality of desert birds appears higher than in some other temperate communities. The lower nesting success may be compensated by a longer potential breeding season, at least in the warmer deserts. Desert rodents of the genus *Perognathus* have a longer life span and lower mortality rate than other rodents, owing apparently to a relatively low basal metabolism, and periodic torpor at times of food shortage and cold.

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